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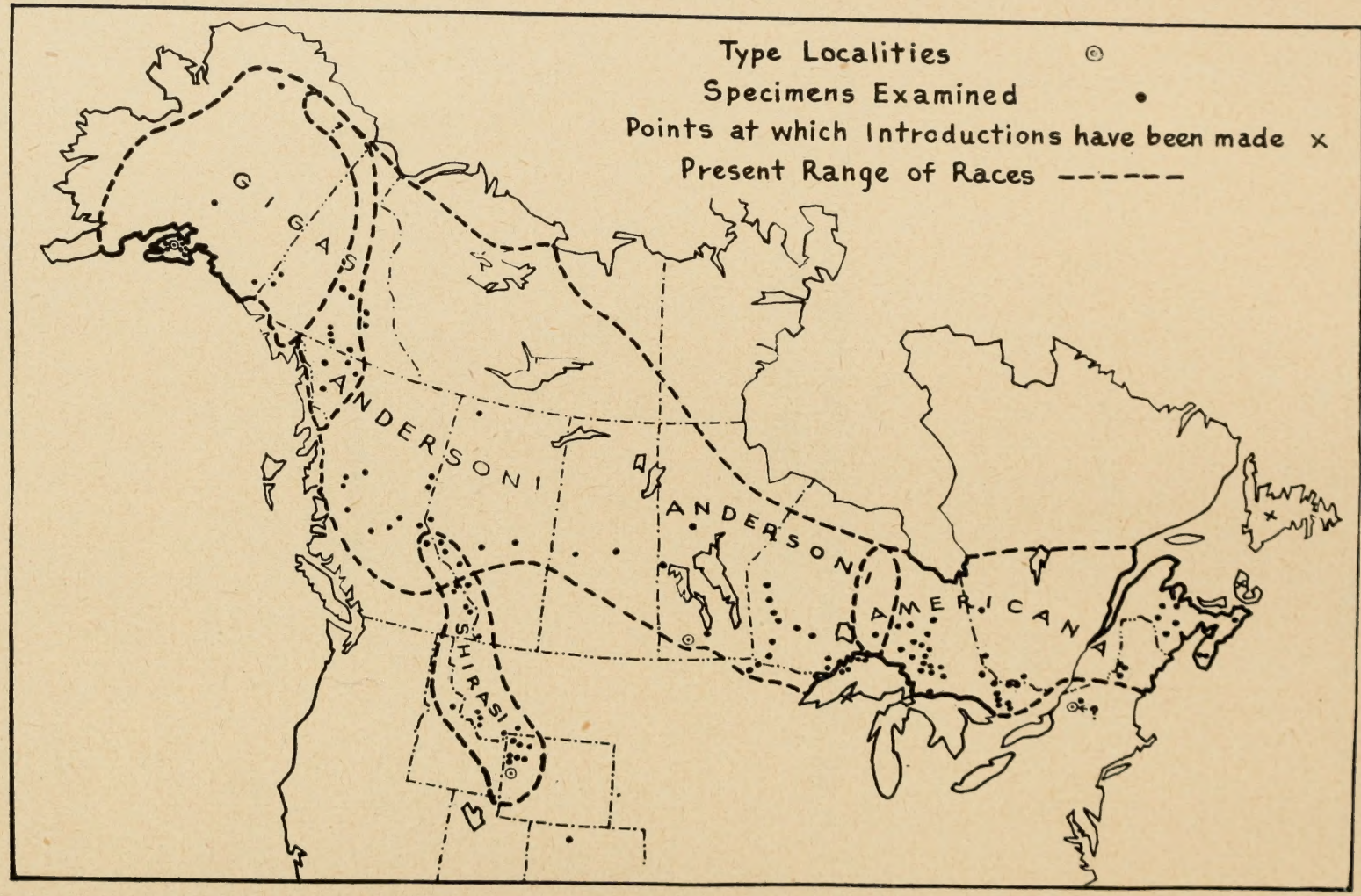

FIG. 1. Map showing the distribution of moose in North America with localities from which specimens have been examined.

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RANDOLPH L. PETERSON

THE GENUS *Alces* (North American moose and Old World elk) has never been satisfactorily revised. Taxonomic treatments of the New World moose have been restricted to descriptions of new forms without any serious attempt to evaluate the relationships of these races with those of the Old World. Unfortunately, the present attempt to consider all the modern representatives of this genus is seriously handicapped by the lack of adequate series of specimens from the Old World and the paucity of available taxonomic literature dealing with these forms. The most recent revision of the Old World elk or moose available to the author is that of Flerov (1931) who bases his review on a series of some sixty skulls of the genus *Alces*. The present treatment is based on a study of 304 specimens (mostly skulls), seven skulls representing two Old World forms and 297 specimens from North America.

ACKNOWLEDGMENTS

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I also wish to express my appreciation to Messrs T. M. Shortt, Eric Thorn and Archie Reid for the preparation of illustrations.

Quotations from Allen (1940) have been made with permission of the American Museum of Natural History.

Explanations

Measurements. All measurements of specimens are given in millimeters. The following are cranial measurements which have been recorded in table I and found to be the most useful ones from a set of 44 which were recorded for each complete skull examined.

Greatest length—Length from anterior tip of premaxillae to the posterior point of the occiput.

Median palatal length—Length from anterior tip of premaxillae to the median posterior edge of the palate.

Length of rostrum—Length from anterior tip of premaxillae to anterior rim of orbit.

Length of nasal aperture—Length from anterior tip of premaxillae to junction of nasal and maxillary bones.

Mastoid breadth—Greatest transverse dimension of skull across mastoid process; outside of one to outside of the other.

Height of occiput—Vertical dimension from the inion to the lower lip of the foramen magnum.

Length of upper toothrow crowns—Greatest distance from the anteriormost edge of the crown of the first premolar to the posteriormost edge of the crown of the last molar.

Greatest width of palate between toothrows—Greatest width between third upper molars at the margins of the alveoli.

Least width of palate between toothrows—Least width between first upper premolars at the margins of the alveoli.

"Per cent flare" of nasal aperture—An expression of the shape of the nasal aperture derived by subtracting the measurement of the width of the nasal aperture at the junctions of the nasal and maxillary bones from the measurement of the greatest inside width of the nasal aperture (along the dorsal rim) and calculating the difference in terms of its percentage of the length of the nasal aperture.

Nature of material studied. Special emphasis has been placed on cranial characters and a majority of the specimens examined are represented by skulls only. Skins were examined where available and direct colour notes were recorded using Ridgway's "Color Standards and Nomenclature, 1912." Where possible, comparable skins (of the same season) of the various races were compared directly with one another.

Intergrading specimens. Specimens which showed evidence of possible intergradation are listed under "Remarks" under *A. a. andersoni* rather than under the "specimens examined" section of the race to which they might seem best assignable.

Abbreviations of institutions. Institutions containing the specimens examined are abbreviated as follows:

Academy of Natural Sciences, Philadelphia—A.N.S.P.; American Museum of Natural History—A.M.N.H.; Biological Surveys Collection (U.S. Fish and Wildlife Service)—B.S.C.; British Columbia Provincial Museum—B.C.P.M.; Carnegie Museum—Carn.M.; Chicago Natural History Museum—C.N.H.M.; Denver Museum of Natural History—D.M.N.H.; Montana State College—M.S.C.; Museum of Comparative Zoology, Harvard University—M.C.Z.; National Museum of Canada—N.M.C.; Royal Ontario Museum of Zoology and Palaeontology—R.O.M.Z.P.; United States National Museum—U.S.N.M.; University of British Columbia—U.B.C.; University of Kansas, Museum of Natural History—U.Kan.; University of Michigan, Museum of Zoology—U. Mich.; University of Montana—U. Mont.; Yellowstone National Park—Y.N.P.

Variation

Sexual variation. The variation between sexes of moose is so great that separate treatments must be made. In addition to averaging larger, the males bear antlers which result in certain modifications of the skull.

Individual variation. The extent of divergence from the mean exhibited in a series of specimens is quite wide in moose. In order to evaluate the variation found in such a wide ranging species, calculations of the standard errors and the standard deviations have been made for both sexes of the middle-aged specimens studied (see fig. 2). The observed limits of the range of variation are also given for the three age groups of adult males examined (see table I).

Variation with age. The range in size variation is so great in skull measurements for animals the size of moose that many criteria must be defined in terms of relative proportions. There are, nevertheless, changes in both direct sizes and relative proportions as the animal grows older; for this reason it has

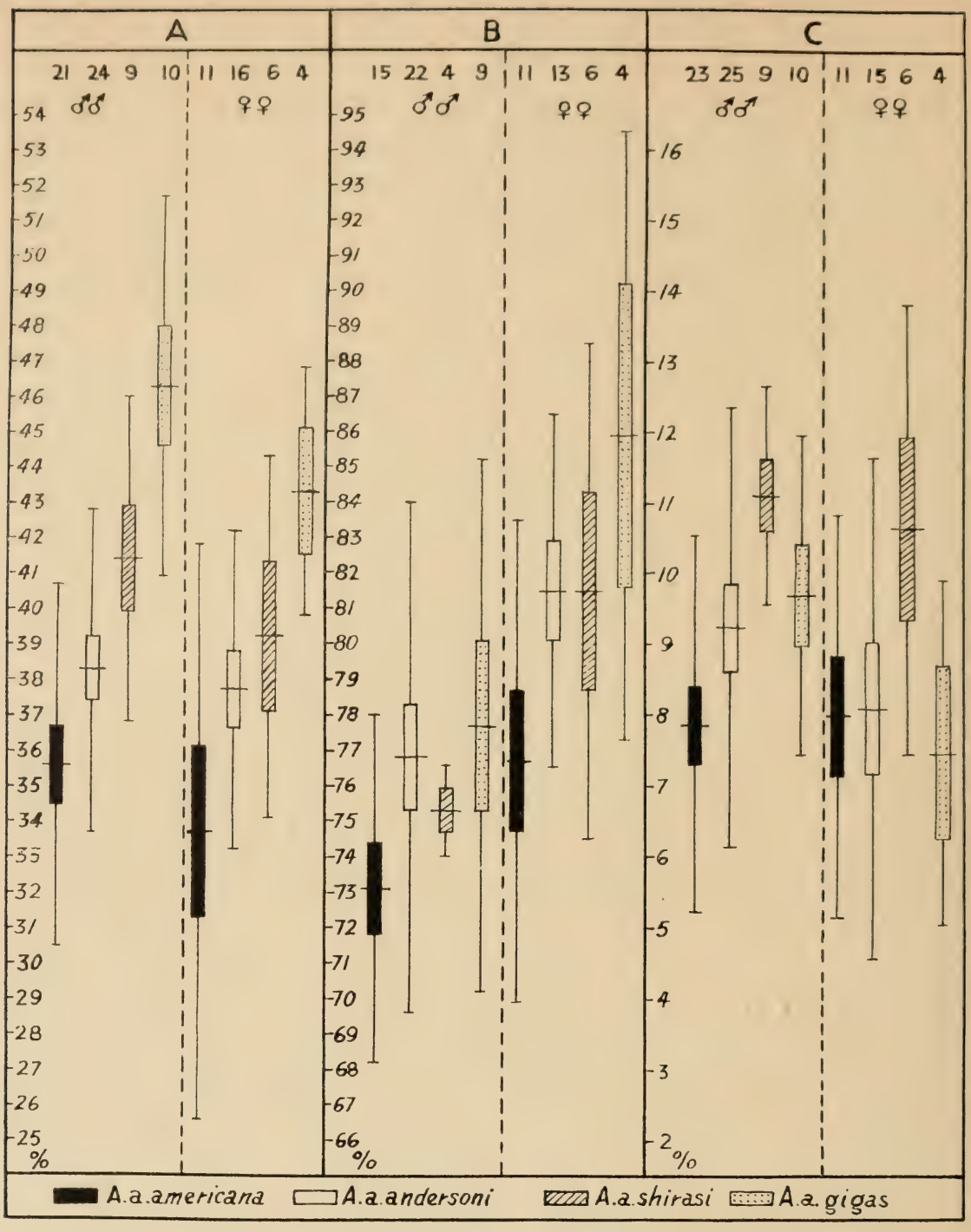

FIG. 2. Variation in skull characters of North American moose. Median horizontal bars represent the mean, the central enclosed areas represent two standard errors

$$\left(SE = \frac{S}{\sqrt{N}}\right)$$

and the median vertical lines represent two standard deviations on either side of the mean

$$\left(S = \sqrt{\frac{\Sigma x^2}{N-1}}\right).$$

Figures above indicate number of specimens in each sample.

A. Ratio of the least width of the palate (between toothrows) to the length of upper toothrow crowns.

B. Ratio of the height of the occiput (inion to the lower lip of the foramen magnum) to the mastoid width.

C. Ratio of the difference between the greatest inside width of the nasal aperture and the width of the aperture at the junction of the nasals, to the length of the nasal aperture.

seemed necessary to separate all adult specimens (above two years of age) into three categories—young adults, middle-aged adults, and old adults. This classification is based on the degree of wearing on the dentition. Specimens showing little or no wear on the teeth, especially the first lower premolar, are regarded as young adults. Those exhibiting moderate wearing on the dentition are considered middle-aged adults; while well or excessively worn dentitions are classed as old adults. Within these groups, the young adults obviously show the most striking variations. It is extremely difficult to obtain comparative samples containing equal representations of the various stages of development within this age group because of the rapid growth rate during this period.

In table I, showing some of the variations found in cranial measurements of the various races of moose, the series of *A. a. andersoni* being the largest, seems to give the most adequate representation of the variations found within the three age groups considered. Here it can be seen that considerable growth takes place during the young adult stage, with little or no increase beyond this middle-aged group.

With respect to the dentition, however, there is continued decrease in the length of the upper toothrow crowns as the animals grow older. This seems almost directly attributable to wearing away of the crowns through use.

With the decrease in the length of the toothrow, it necessarily follows that there is a change with age of such useful taxonomic characters as the relative widths of the palate compared to the length of the toothrow.

The ratio of the least width of the palate, between the toothrows, to the length of the upper toothrow crowns, showed a consistent increase with age in all groups examined.

A change with age in the shape of the occiput is also evident in the males of all races represented. The height of the occiput increases slowly from the young adult stage onward, while the mastoid width increases markedly between the young and middle-aged adult groups. Undoubtedly, a part of this change is correlated with the development of antlers, and the required modification for their support. Similar trends were also noted in a smaller series of *A. a. andersoni* females, but in this case the changes were less marked.

Geographic variation. There has been considerable disagreement concerning the number of valid species that should be recognized for this genus. Lydekker (1915) recognized only one

TABLE I.—Cranial measurements of moose. The mean is followed by th

	♂ *A. a. americana*			♂ *A. a. andersoni*		
	Young ad.	Mid-ad.	Old ad.	Young ad.	Mid-ad.	Old
Greatest length	578.0 (5) (554–590)	**605.9** (21) (574–660)	599.3 (3) (590–610)	569.5 (11) (538–586)	**591.7** (24) (559–621)	593. (576
Median palatal length	339.3 (3) (321–357)	**360.4** (17) (342–394)	351.0 (2) (344–358)	335.5 (11) (309–350)	**349.7** (24) (331–368)	350 (334
Length of rostrum	351.6 (5) (338–370)	**370.7** (23) (348–398)	371.5 (4) (356–387)	347.5 (11) (326–363)	**360.7** (25) (335–382)	360 (346
Length of nasal aperture	253.2 (5) (238–263)	**275.7** (23) (258–294)	276.0 (4) (261–286)	249.5 (11) (229–260)	**265.0** (25) (248–292)	267 (255
Mastoid breadth	149.7 (4) (145–155)	**168.6** (21) (156–177)	167.0 (3) (166–169)	150.4 (11) (139–162)	**164.0** (25) (157–176)	164. (152
Height of occiput	118.0 (3) (115–120)	**121.7** (15) (110–129)	122.0 (2) (121–123)	120.8 (9) (115–124)	**125.2** (22) (115–134)	124. (118
Ratio of height of occiput to mastoid breadth (%)	78.1 (2) (76.8–79.4)	**73.1** (15) (70.4–75.8)	72.8 (2) (71.6–74.0)	80.0 (9) (72.5–86.3)	**76.8** (22) (68.8–85.2)	75.7 (72.0
Length of upper toothrow crowns	150.6 (5) (145–157)	**152.6** (24) (147–162)	148.7 (3) (146–153)	152.9 (11) (149–156)	**149.8** (24) (144–158)	146. (140
Greatest width of palate between toothrows	83.3 (3) (80–88)	**89.1** (21) (80–97)	87.0 (2) (85–89)	83.4 (11) (78–88)	**90.3** (25) (81–100)	90.3 (84
Ratio greatest width of palate (between toothrows) to length of upper toothrow crowns (%)	55.4 (3) (53.4–57.2)	**58.4** (21) (53.0–63.7)	58.0 (2) (57.9–58.1)	54.6 (11) (51.0–57.5)	**60.3** (24) (55.5–66.4)	62.0 (57.2
Least width of palate between toothrows	52.6 (3) (52–54)	**54.7** (21) (48–62)	54.0 (2) (53–55)	54.5 (11) (51–60)	**57.4** (25) (53–65)	58.1 (52
Ratio least width of palate between toothrows to length of upper toothrow crowns (%)	35.0 (3) (33.8–36.8)	**35.6** (21) (31.0–40.7)	36.0 (2)	35.7 (11) (33.3–39.0)	**38.3** (24) (33.6–43.0)	39.9 (35.6
"Per cent flare" of nasal aperture	8.00 (5) (6.49–9.49)	**7.88** (23) (6.02–10.64)	7.02 (4) (4.60–9.10)	8.53 (11) (6.42–10.29)	**9.25** (25) (6.24–13.25)	8.7 (7.60

specimens examined (in parentheses) with the observed limits given below.

♂ *A. a. shirasi*			♂ *A. a. gigas*		♂ *A. a. pfizenmayeri*		♂ *A.a.alces*
g ad.	Mid-ad.	Old ad.	Mid-ad.	Old ad.	Mid-ad.	Old ad.	Mid-ad.
(1) .	**601.0** (7) (577–634)	579.2 (5) (569–594)	**633.8** (11) (601–661)	650.0 (4) (616–686)	**596.0** (2) (587–605)	621 (1)	574 (1) . . . .
(2) 343)	**344.0** (7) (324–379)	333.8 (5) (322–344)	**361.2** (9) (355–382)	375.5 (4) (351–390)	**345.0** (2) (343–347)	371 (1)	349 (1) . . . .
(2) 352)	**338.4** (9) (334–386)	349.5 (5) (333–359)	**381.2** (11) (364–410)	389.0 (5) (363–408)	**360.5** (2) (358–363)	379 (1)	349 (1) . . . .
(2) 249)	**267.4** (9) (251–293)	257.5 (5) (254–264)	**284.4** (11) (263–297)	291.6 (4) (275–300)	**267.5** (2) (266–269)	287 (1)	242 (1) . . . .
1) .	**160.9** (10) (145–169)	164.7 (6) (160–174)	**172.5** (11) (163–181)	172.5 (4) (165–183)	**157.5** (2) (156–159)	176 (1)	**159** (2) . . . .
1) .	**122.8** (4) (118–127)	121.2 (6) (115–127)	**134.1** (9) (128–140)	132.8 (4) (126–144)	**120.2** (2) (118–122)	131 (1)	**124.5** (2) (119–130)
. .	**75.3** (4) (74.7–76.2)	73.5 (6) (69.6–76.6)	**77.7** (9) (72.7–83.2)	77.4 (4) (74.0–78.6)	**76.1** (2) (75.6–76.6)	74.4 (1)	74.7 (1) . . . .
(2) 44)	**142.9** (11) (136–151)	140.8 (6) (138–145)	**147.5** (11) (142–155)	145.4 (5) (141–149)	**145.5** (2) (143–148)	147 (1)	**149.7** (3) (144–153)
2) 86)	**88.1** (9) (85–91)	90.3 (6) (85–94)	**95.9** (10) (92–101)	97.2 (5) (90–106)	**92.5** (2) (92–93)	102 (1)	**94.0** (2) (90–98)
2) 59.7)	**61.2** (9) (57.3–66.9)	64.2 (6) (60.3–67.6)	**65.1** (10) (60.0–67.8)	66.8 (5) (62.4–71.6)	**63.6** (2) (62.8–64.4)	69.5 (1)	**63.5** (2) (62.5–64.5)
2) 9)	**59.2** (9) (53–63)	61.5 (6) (56–67)	**68.0** (10) (62–71)	72.4 (5) (61–80)	**66.5** (2) (65–68)	69 (1)	**62.0** (2) (60–64)
2) 1.0)	**41.4** (9) (37.3–44.8)	43.7 (6) (40.0–46.2)	**46.3** (10) (40.0–49.0)	49.9 (5) (40.8–54.1)	**45.8** (2) (43.9–47.6)	47.0 (1)	**41.9** (2) (41.7–42.1)
(2) 2.05)	**11.11** (9) (10.10-12.36)	11.59 (4) (9.26-12.60)	**9.70** (10) (7.67–11.50)	10.01 (4) (9.32–11.35)	**8.78** (2) (8.17–9.40)	9.05 (1)	8.25 (1) . . . .

species (*A. alces*). However, most North American authors have continued to recognize from one to three New World species as distinct from the Eurasian forms. Lydekker (1915) listed two races for the Old World and three for North America, not including *A. a. shirasi*. Flerov (1931) reviewed the Old World forms and supported Lydekker's theory that both Old and New World forms are conspecific. Further acceptance has been made by Allen (1940), Hall (1946) and others. Flerov (1931) concludes that Lydekker's description of *A. bedfordiae* is not diagnostic of any race of moose and that *A. a. pfizenmayeri* should be the name applied to the elk of northern and central Siberia. He describes a small specimen from the Amur River region along the Manchurian border which he regards as different from other Old World races although he does not give it a distinct name. Allen (1940) has shown that *Cervus cameloides* was applied to elk from Manchuria by Milne-Edwards in 1867 and thus provides the earliest available name for an eastern Asiatic race. Milne-Edwards' description was again based on one or perhaps more antlers and it is therefore difficult to assign diagnostic features. It therefore seems possible that a third race may occur, or has occurred, in the Amur River region of southern Siberia, northern Mongolia and northern Manchuria which would bear the name *Alces alces cameloides* (see fig. 5). Unfortunately I have been unable to examine material from this region and therefore cannot determine the validity of its status. If it is not a distinct race the name may prove available for all the elk of eastern Asia. In this treatment I have followed Flerov in considering the northern Asiatic animals as *pfizenmayeri* with the possibility that the elk of the Amur River region represent a smaller distinct race, *cameloides*.

In a preliminary review of North American moose (Peterson, 1950) it was felt that insufficient Old World specimens were available to properly evaluate the status of the relationships between *A. americana* and *A. alces*. A more thorough study of three available skulls of *A. a. pfizenmayeri* and data presented by Flerov (1931) indicate a close relationship between that race and *A. a. gigas*. Since there seems little justification for separating the North American moose as a distinct species, one is compelled to agree with Lydekker and Flerov that it should be regarded as conspecific with *Alces alces*.

The North American moose are divided into four geographic races. In fig. 2, showing a statistical treatment of three cranial characters, a general east-west cline is evident in such characters

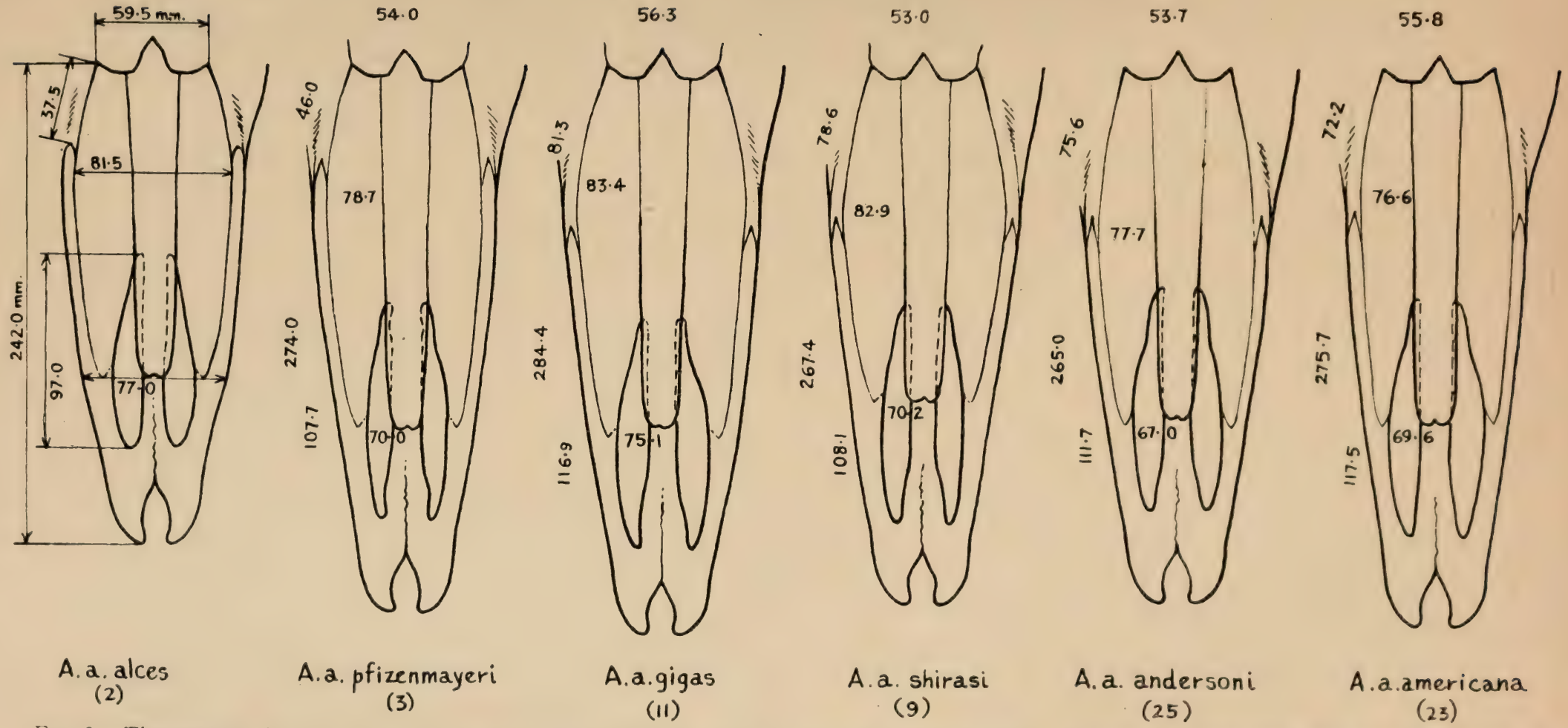

FIG. 3. The average size and shape of the nasal apertures of the races of *Alces alces* (adult bulls). Figures in parenthesis refer to the number of specimens averaged.

as the ratio of the least width of the palate between the toothrows to the length of the upper toothrow crowns. In these statistical treatments specimens from near the zone of overlap of the geographical races (i.e., British Columbia and Yukon Territory) were not included in the samples.

The largest North American race is the Alaskan form (*A. a. gigas*). The more southerly races average smaller but do not appear significantly different from each other, although the greatest length of the skull of *A. a. americana* specimens examined averaged slightly longer than the other two.

The general shapes of the nasal aperture and the premaxilla-maxilla complex have proved useful in distinguishing the various races of *Alces alces*. A diagramatic drawing showing the average shapes and measurements of this pre-nasal complex is shown in fig. 3 for the middle-aged adult males examined.

The shape of the palate as expressed by the ratio of the least width of the palate between the toothrows to the length of the upper toothrow crowns is perhaps one of the best characters for distinguishing the geographic races of *Alces alces* (see figs. 2A and 4).

Palaeontological History

The order Artiodactyla, to which the moose belongs, has been traced back to the lower Eocene, although it did not reach its greatest diversity in numbers and importance until the Pleistocene or later. Scott (1937) has pointed out the close relationships of certain Old World and New World members of the family Cervidae in the northern hemisphere, namely wapiti (*Cervus*), moose (*Alces*) and the caribou (*Rangifer*). He states (p. 322):

> None of these has been found in America in deposits older than the Pleistocene, nor anything that could be ancestral to them; they were all very late immigrants from Asia.
>
> At least one Pleistocene genus, the Stag-moose (*Cervalces*) was different from any now living. The only known skeleton, now in the Princeton Museum, is in Pleistocene deposits. The skeleton of *Cervalces* is very much like that of the Moose; the bones of the neck, trunk and limbs are almost identical in the two genera, but skull and antlers are very different. The nasal bones are much less shortened than in the Moose, an indication that the proboscis-like muzzle was less inflated. The antlers are unique, though in a general way like those of *Alce*, they are much less palmated and they have, in addition, a great trumpet-like plate of bone on the lower side of each antler; this plate is not known in any other member of the Cervidae. *Cervalces* has not been found in the Old World, yet it must have originated there from the same stock as the Moose and accompanied the latter in its migration to North America.

Thus far *Cervalces* has been taken from Kentucky, New Jersey, Iowa, Nebraska, Ontario and Alaska (Frick, 1937). Earlier, Hay (1924) reported this genus from Missouri, Oklahoma, Virginia, Illinois and Pennsylvania. Discussing *Cervalces scotti* from New Jersey, Hay (1923, p. 306) makes the following statement: "It seems certain, therefore, that this stately relative of our existing moose lived after the disappearance of the Wis-

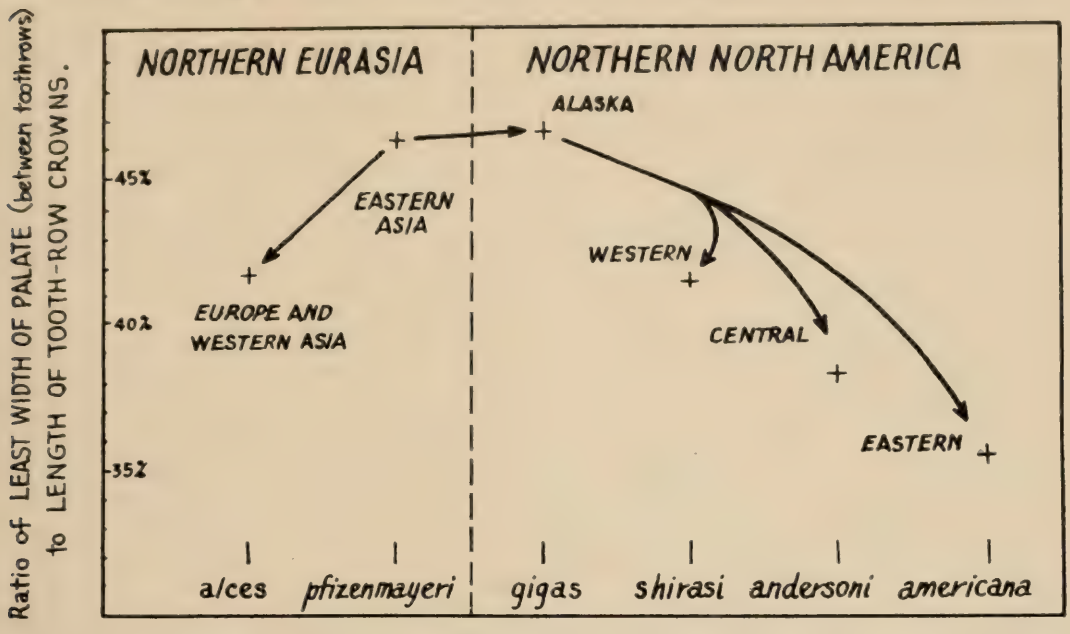

FIG. 4. Geographical relationships of the races of *Alces alces* as indicated by the average relative shapes of the palates.

consin ice-sheet." Frick (1937) reports that *Cervus*, *Alces*, *Cervalces* and *Rangifer* have been taken from the deeply-frozen deposits that overlie the auriferous gravels of the Fairbanks area, Alaska.

Moose (*Alces*) have also been reported from Quaternary deposits in the eastern, central and western regions of the United States and Ontario (Frick, 1937). Hay lists fossil records for the following states: Pennsylvania, Illinois, South Carolina (1923); Minnesota, Oklahoma, Iowa (1924); and Ohio and Washington (1927). These records are sufficient to indicate a wide southerly distribution at one time during the Pleistocene. Some of these specimens have been referred to as *A. americana*, while others have been considered as various extinct species.

The ancestry of *Alces* in the Old World is still uncertain. In recent years various authors have discussed fossil records and applied a confusing array of species to this genus (*Alces* and *Alce*) including *alces*, *fossilis*, *gigantea*, *latifrons*, *machlis* and *palmatus*. Of these names, used since 1933, some are obviously

synonyms of *Alces alces* and one belongs to another genus entirely. Reynolds (1934) reviews the genus in Great Britain and discusses its occurrence on the European continent as follows (p. 9):

> . . . the elk existed on the Continent all through post-glacial times, and [records] show that in prehistoric and late Pleistocene times it ranged all over Northern and Central Europe, extending as far south as Roumania, Northern Italy and the Pyrenees. Its distribution corresponded closely with that of the reindeer. But while, as Boule remarks, the reindeer accompanied the retreating ice, leaving France before the dawn of recent conditions, the elk persisted longer in Central and Western Europe, and its complete disappearance from this region seems more likely to be due to human agency than to climatic change. In the time of Julius Caesar it was abundant in the Black and Hercynian Forests, and was to be found in Bavaria in the Eighth Century and in Flanders in the Tenth. It is still living in East Prussia, and is found in increasing numbers in Finland, Sweden and Norway, and throughout Northern Asia as far as the Pacific.

A study of the available living forms suggests that Asia was probably the centre of dispersal with *pfizenmayeri* approaching the ancestral type. Westward dispersal gave rise to perhaps the smallest existing race (*alces*) which is characterized by a unique development in the species of a much elongated and broadened nasal extension of the premaxilla. A third form may have moved south into Mongolia and Manchuria (*A. a. cameloides*) but detailed knowledge of this supposed race must await further study. Dispersal eastward resulted in more-or-less gradual and progressive diversions from the ancestral type. In such characters as the relative shape of the palate the affinities of *pfizenmayeri* and *gigas* are more similar than any other two geographically-adjacent races (see fig. 4). The Alaskan moose (*Alces alces gigas*) may have existed in the unglaciated regions of Alaska throughout the latter stages of Pleistocene glaciation. On the other hand, it may be a much later immigrant than the more southern North American races.

Diagnosis of the Genus

Genus ALCES Gray
Moose, Old World Elk

1821. *Alces* Gray, London Med. Repos., vol. 15, p. 307.
1827. *Alce*, H. Smith, Griffith's Animal Kingdom, vol. 4, p. 72; vol. 5, p. 303.
1841. *Alcelaphus* Gloger, Handbuch Naturgeschichte, p. 143 *nec* Blainville, 1816.
1857. *Alces* Blasius, Saugethiere Deutschlands, p. 34.

1902. *Paralces* Allen, Bull. Amer. Mus. Nat. Hist., vol. 16, p. 160. (Substitute for *Alces* proposed on the assumption that this is a homonym of *Alce* Blumenbach, 1799.)

1945. *Alce* Simpson, Bull. Am. Mus. Nat. Hist., vol. 85, p. 155. (Proposes acceptance of *Alce* Frisch, 1775.)

1948. *Alces* Hershkovitz, Jour. Mamm., vol. 29, no. 3, p. 273. (Shows *Alce* Frisch, 1775 to be non-Linnaean and unavailable; *Alces* Gray, 1821, should stand.)

Type Species. *Cervus alces* Linnaeus.

Geographical distribution. Circumpolar in the boreal coniferous forests of both the Old and the New World (see fig. 5).

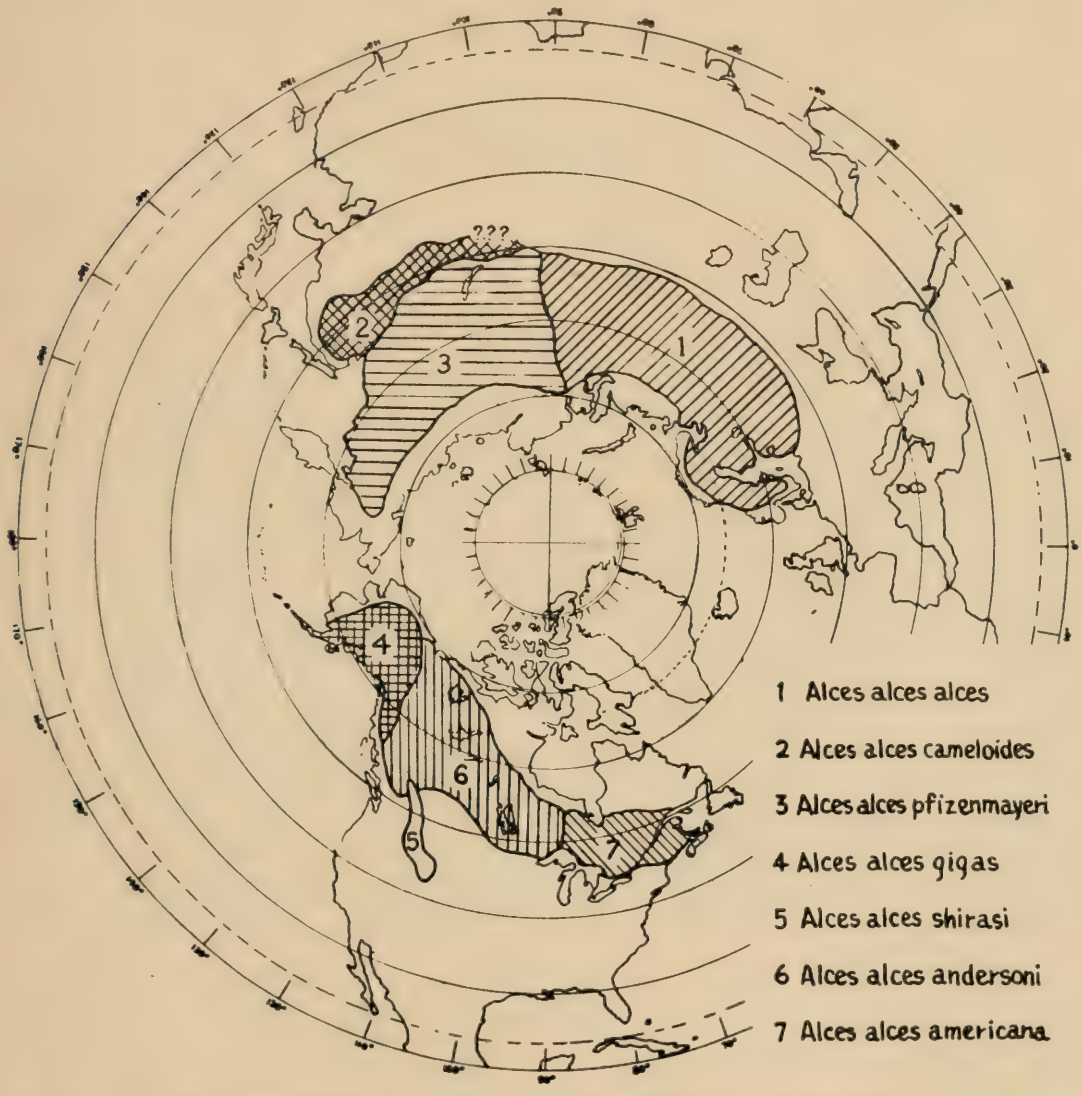

FIG. 5. Map showing the world-wide distribution of *Alces alces*.

Characters. The moose (and Old World elk) is readily distinguished by its large size (about the size of a saddle horse; the largest living Cervid), heavy body, long legs, high shoulder

region, short tail, broad overhanging muzzle, large ears, short neck and unique dewlap or "bell". The nose is covered with short hair except for a bare spot between the nostrils which is usually more or less triangular in shape. Adult males develop extremely large antlers which are characteristically broad palmate blades with projecting tines.

The upper part of the body is quite dark in new spring pelage, appearing almost black in some individuals, and in others varying towards dark brown, reddish brown and grayish brown. The underparts of the belly and lower legs are distinctly lighter, usually either grayish or brownish in colour, sometimes almost whitish. There is a gradual fading in body colour during summer, fall and winter to produce a more grayish effect by early spring.

In addition to general characters given above, *Alces* may be distinguished by skull greatly lengthened in premaxillary region; nasal region shortened with sizable nasal aperture; distance from front of nasal to front of premaxilla about equal to that from back of nasal to back of occiput; vomer lower posteriorly, not dividing aperture of posterior nares; lacrimal vacuity widely open, the pit well developed, maxillary canines usually absent in both sexes; lower canines incisiform, incisors but little differentiated; molars and premolars rather broad and low crowned. Median metacarpals united as a cannon bone; lateral metacarpals strongly attenuated, rudimentary, with only distal ends developed as styloid vestiges (teleometacarpalian). Metatarsal gland absent; front hoofs larger than posterior ones, both long, narrow and pointed.

ALCES ALCES ALCES (Linnaeus)
European Elk

1758. *Cervus alces* Linnaeus, Syst. Nat., I, 10th ed., p. 66.
1910. *Alces machlis typicus* Ward, Records of Big Game, 6th ed., p. 66.
1913. *Alces machlis uralensis* Matschie, Beroff. Institute Jugdkunde, vol. 2, p. 155.
1913. *Alces machlis meridionalis* Matschie, *op. cit.*, p. 156.
1914. *Alces machlis tymensie* Zukowsky, Archiv. f. Naturgeschichte, 80 Jahry., Abt. A.N. 9, p. 42.
1914. *Alces machlis angusticephalus* Zukowsky, *op. cit.*, p. 44.
1915. *Alces alces alces* Lydekker, Cat. Ungulate Mamm. Brit. Mus. (Nat. Hist.), vol. 4, p. 232.

Type specimen. Unknown.
Type locality. Sweden.
Geographical distribution. Northern Europe and western

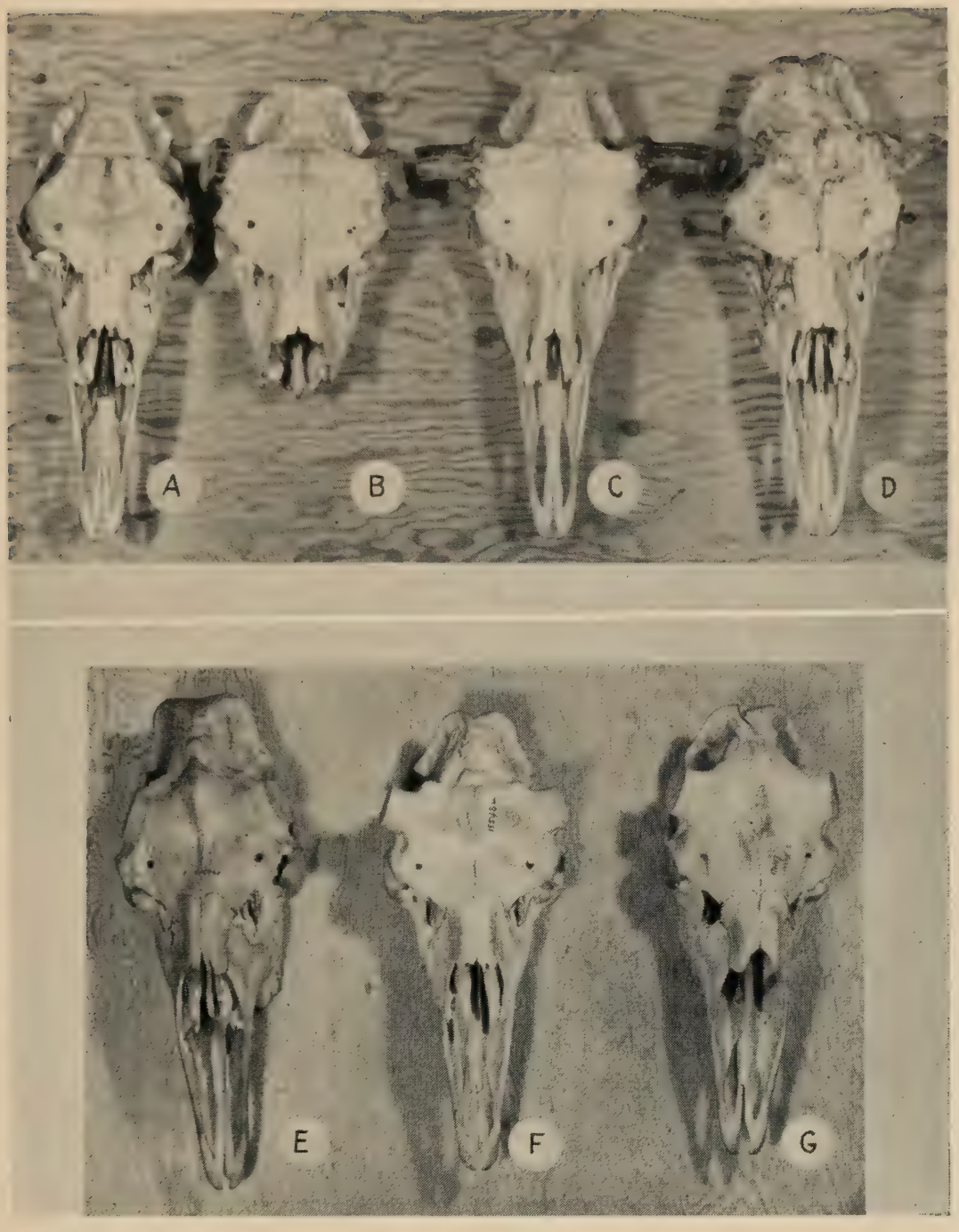

FIG. 6. Skulls (dorsal view) of six races of *Alces alces*.

A. *A. a. americana*, adult female, R.O.M.Z.P. no. 19566 from Hayward Twp., Algoma Dist., Ontario, total length, 587 mm.; B. *A. a. americana*, adult male, R.O.M.Z.P., no. 19551, from Twp. 11-G, Sudbury Dist., Ontario; C. *A. a. andersoni*, adult male, R.O.M.Z.P., no. 19548, from Overflowing River, Manitoba, t.l. 604 mm.; D. *A. a. shirasi*, adult male, U. Mich., no. 64015, from Wyoming, t.l. 616 mm.; E. *A. a. gigas*, adult male, U.S.N.M., no. 140363, from Hope City, Alaska, t.l. 629 mm.; F. *A. a. pfizenmayeri*, adult male, U.S.N.M., no. 155484, from Junction of Aldan and Lena Rivers, Russia, t.l.587 mm.; G. *A. a. alces*, adult male, U.S.N.M., no. 196347, from Trondhjem, Norway, t.l. 574 mm.

Siberia, eastward probably as far as the Yenisey River and Altai Mountains (Flerov, 1931).

Characters. Flerov (1931) gave the following criteria for distinguishing this race from *A. a. pfizenmayeri* (p. 72): (1) Length of skull (adult male) from 550 to 580 mm. (2) Length of the rostrum (from the anterior edge of the orbit, to the end of the intermaxillars) of the adult male from 329 to 347 mm. (3) Palatal processes of intermaxillar bone are narrow above, forwards of vomer, and form a spout-shaped concavity; their width is smaller than the vertical diameter of infraorbital foramen. (4) Nasal processes of intermaxillar bone not narrowed upwards, but are widened spade-like with a blunt end. (5) Colouring greyish brown not passing into blackish tints; the limbs of a lighter colour.

Remarks. An expanded list of synonyms for the species Alces is given by Lydekker (1915). Cranial measurements for two specimens are given by Miller (1912, p. 984). The shape of the nasal process of the premaxillary bone seems distinct enough to distinguish this race from all others. In four specimens examined, the nasal process of the premaxilla extended to within 37.5 mm. (15 to 52) of the nasals. In similar measurements of three specimens *A. a. pfizenmayeri*; the average was 46.0 mm. (42 to 50) while the North American races (mid-adult bulls) averaged as follows: *A. a. americana*, 72.2; *A. a. andersoni*, 75.6; *A. a. shirasi*, 78.6 and *A. a. gigas*, 81.3 (see fig. 3).

Specimens Examined. A total of four as follows:

Norway: Trodhiem, 1 (U.S.N.M.); no definite locality, 1 (M.C.Z.).
Finland: Near Karstula, 1 (M.C.Z.).
Russia: Vicinity of Leningrad, 1 (A.M.N.H.).

ALCES ALCES CAMELOIDES (Milne-Edwards)
Manchurian Elk

1867. *Cervus cameloides* Milne-Edwards, Ann. Sci. Nat., Zool. ser. 5, vol. 7, p. 377.

1868–74. *Cervus alces* Milne-Edwards, Recherches pour servir à l'Hist. Nat. des Mammifères, p. 181.

? 1902. *Alces bedfordiae* Lydekker, Proc. Zool. Soc. London, vol. 1, p. 109 (indefinite locality, possibly applies to this form).

? 1908. *Alces machlis bedfordiae* Lydekker, A trip to Pilawin, p. 85.

? 1915. *Alces alces bedfordiae* Lydekker, Cat. Ungulate Mamm., Brit. Mus. (Nat. Hist.), vol. 4, p. 234.

1931. *Alces alces* subsp. ? Flerov, Comptes Rendus de l'Academie des Sci. de l'URSS., p. 74.

1940. *Alces alces cameloides* Allen, Mamm. China and Mongolia, Am. Mus. Nat. Hist., vol. 11, pt. 2, p. 1205.

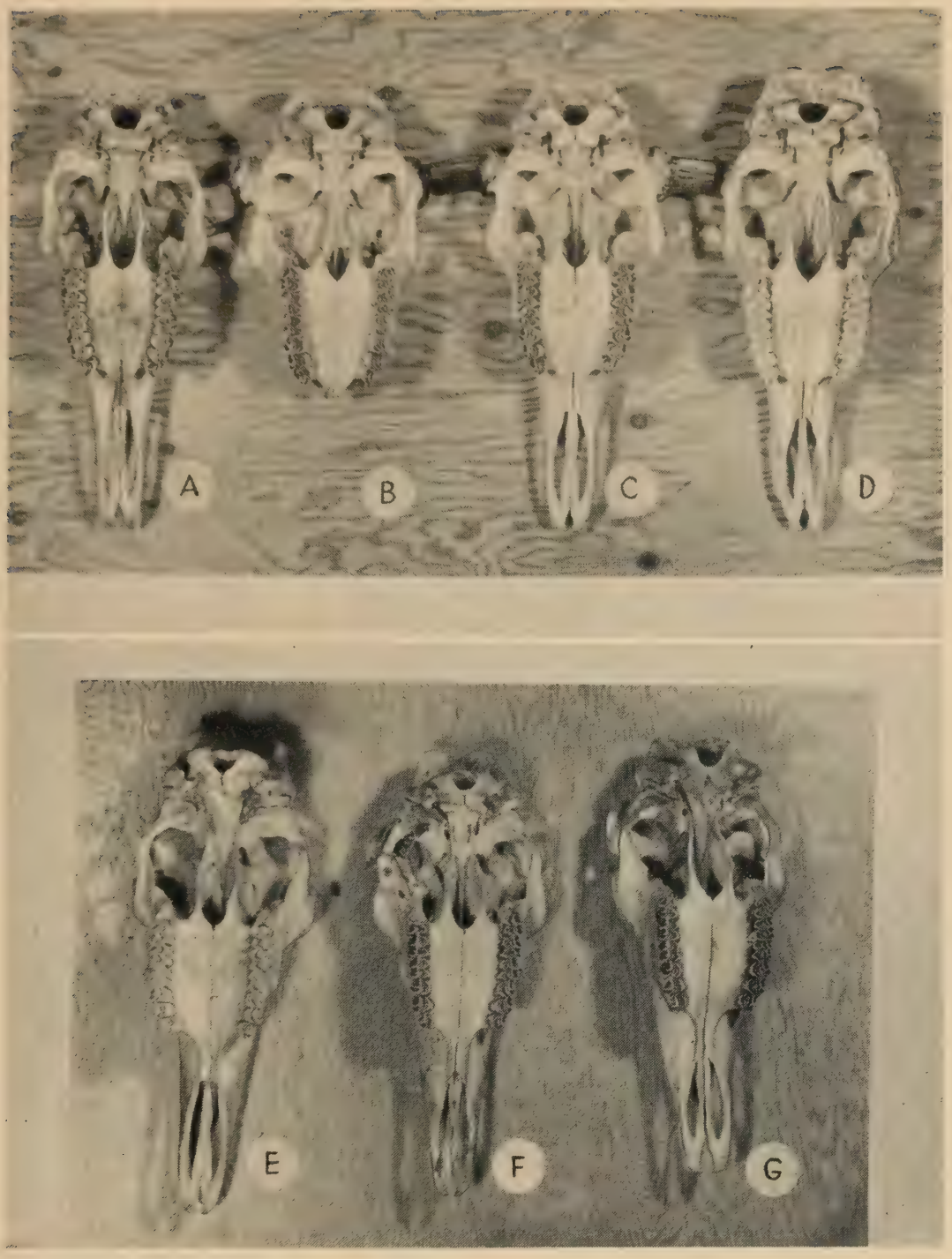

FIG. 7. Skulls (ventral view) of six races of *Alces alces* (same specimens shown in fig. 6).

A. *A. a. americana*, female; B. *A. a. americana*, male; C. *A. a. andersoni*; D. *A. a. shirasi*; E. *A. a. gigas*; F. *A. a. pfizenmayeri*; G. *A. a. alces*.

Type Specimen. Unknown (?). Supposedly one or more antlers in the Paris Museum.

Type Locality. Manchuria (?).

Geographical Distribution. Limits of range unknown. Supposedly from the Amur River region of extreme southeastern Siberia, northern Manchuria and northeastern Mongolia (see fig. 5).

Characters. From the original description Allen (1940, p. 1206) provides the following:

> . . . Milne-Edwards (1867) briefly characterizes some antlers brought back by Fontamer, which, though procured in China, came originally, as he was informed, from Manchuria. These, writes Milne-Edwards, somewhat recall those of a young elk or moose, but appeared to be from adult animals; they were but slightly elevated, and remarkably heavy; the short beam carried an anterior basal tine, which in adults is almost as stout as the main branch and is bifurcate. The palms are very broad, especially in youth. The main beam turns abruptly backward and gives off a second nearly vertical tine.

Concerning a specimen from this same general region, Flerov (1931, p. 74) writes as follows:

> In the collection of the Zoological Museum there is a skull of a semi adult elk from the environs of the Nicolajcuskij post on the Amur, brought by L. Schrenk. By its dimensions it does not exceed the size of the European elk, and is considerably smaller than all the east Siberian elks. The intermaxillare are like those of the eastern elks.

Allen (1940, p. 1205) describes the pelage as follows:

> The skin of an immature female secured by Dr. R. C. Andrews sixty miles northeast of Urga, Mongolia, is a mixed gray and brownish on the cheeks, neck and sides of the back, but the chest and flanks are clearer darker brown and the chin is blackish brown. The forehead and muzzle are tinged with ochraceous, and the feet and legs are similar but slightly darker, becoming brown near the hoofs. A short mane stands erect along the median line of the neck and shoulders and a very small (one inch) "bell" or tuft is present at the throat. It appears paler than the moose of eastern North America.

Remarks. The above references to *Alces* from this region are all based on what each author regards as apparently immature specimens, although Flerov appears to feel that this specimen actually represented a smaller form than *pfizenmayeri*. Without recourse to specimens from this area, I have accepted the possible occurrence of this race largely on the basis of Flerov's recognition of its distinctness. He was apparently unaware of Milne-Edwards' early name available for this race. Adequate material may well reveal that the above mentioned are merely immature specimens of the Siberian race. In such an event, the name *cameloides* would apparently stand.

Specimens Examined. None.

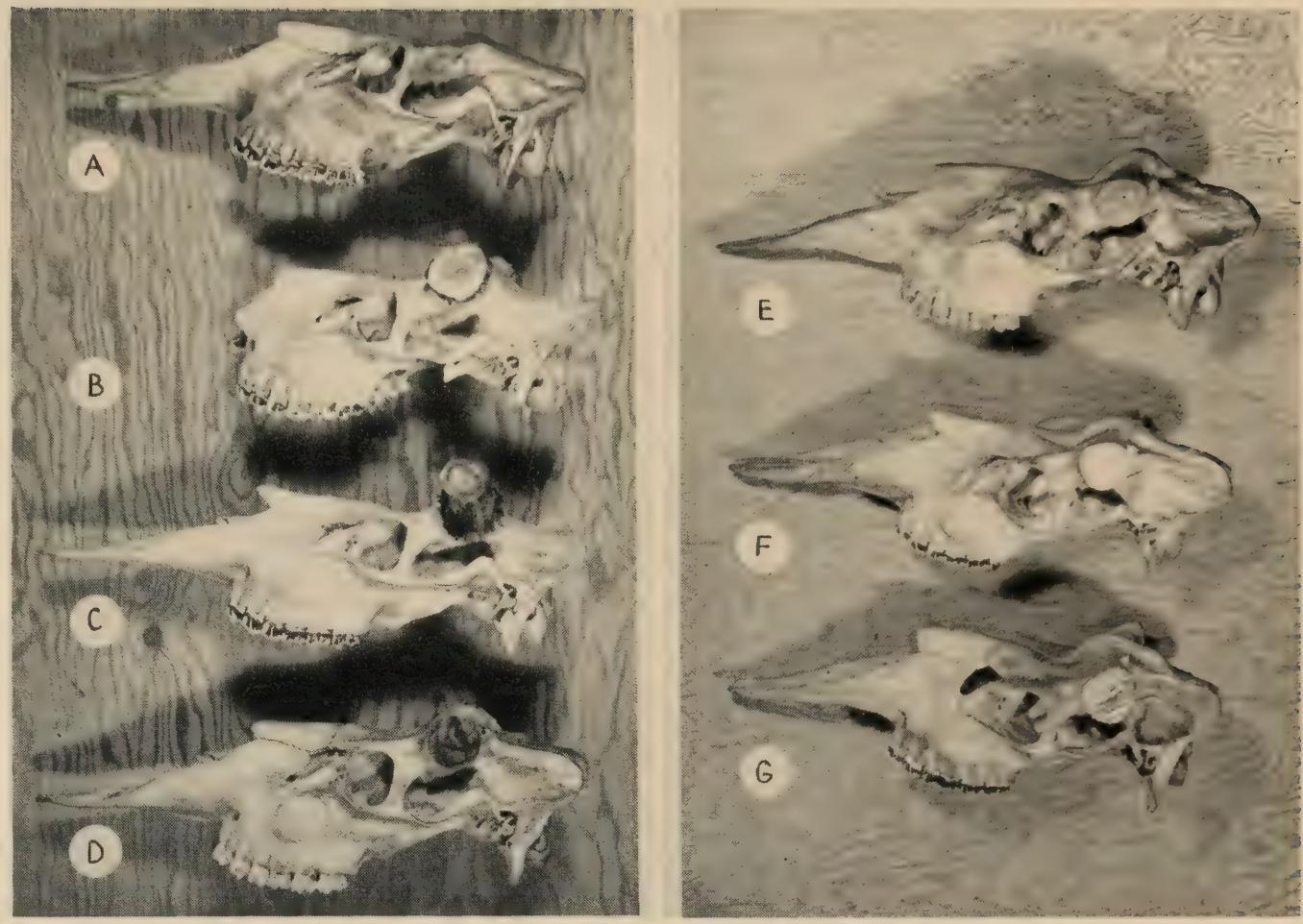

FIG. 8. Skulls (lateral view) of six races of *Alces alces* (same specimens shown in fig. 6).
A. *A. a. americana*, female; B. *A. a. americana*, male; C. *A. a. andersoni*; D. *A. a. shirasi*; E. *A. a. gigas*; F. *A. a. pfizenmayeri*; G. *A. a. alces*.

ALCES ALCES PFIZENMAYERI Zukowsky
Siberian Elk

1910. *Alces pfizenmayeri* Zukowsky, Wild und Rund, 16 Juhrg., Bd. II, p. 807.
? 1902. *Alces bedfordiae* Lydekker, Proc. Zool. Soc. London, vol. 1, p. 109.
? 1908. *Alces machlis bedfordiae* Lydekker, A trip to Pilawin, p. 85.
1911. *Alces machlis jukutakensis* Millais, Field, vol. 118, p. 113.
? 1915. *Alces alces bedfordiae* Lydekker, Cat. Ungulate Mamm. Brit. Mus. (Nat. Hist.), vol. 4, p. 234.
1931. *Alces alces pfizenmayeri* Flerov, Comptes Rendus de l'Academie des Sci. de l'URSS, p. 73.

Type Specimen. Unknown (?).

Type Locality. Aldan River, Yakutia, Russia.

Geographical Distribution. Northern Siberia, eastward from the Yenisey River (Flerov, 1931), probably south to Sayan, Yablonovy and Dzhugdzhur mountain ranges.

Characters. Flerov (1931) gives the following: (1) Length of skull (adult male) from 585 to 620 mm. (2) Length of the rostrum from 359 to 373 mm. (3) Palatal processes of intermaxillar bone are flat and broad, forwards of vomer, and forming no spout-shaped concavity, their width is larger than the vertical diameter of infra-orbital foramen. (4) Nasal processes of intermaxillar bone are gradually narrowed and pointed upwards. (5) Colouring blackish-brown, often very dark (almost black); the limbs may be of a brownish colour.

Remarks. Flerov (1931) suggests the possibility that this form is identical with *A. a. gigas.* In comparing the cranial measurements of these two races (see table I) it becomes apparent that there are several striking similarities. In general *A. a. gigas* averages larger. The total length of the skull averaged 633.8 mm. (601–661) in 11 mid-adult bulls and 650.0 mm. (616–686) in four old-adult males. Similar measurements for *A. a. pfizenmayeri* were 587 and 605 mm. for two mid-adults and 621 for a single old-adult. The length of the rostrum of *A. a. gigas* also appears comparatively longer, averaging 381.2 mm. (364–410) in 11 mid-adult males and 389.0 mm. (363–408) in five old-adults. Specimens of the Siberian race examined, measured 358, 363, and 379 mm., the last, an old-adult, being six millimeters larger than the upper limit listed by Flerov.

On the basis of the material examined, the two races in question appear different with respect to the extension of the nasal process of the premaxilla. In *A. a. pfizenmayeri* this process extended to within 42, 46 and 50 mm. (av. 46.0) of the nasals,

while in *A. a. gigas* the average was 81.3 for both age groups. When this measurement (which represents the dorsal exposure of the maxilla along the nasal aperture) is represented in terms of its length relative to the length of the dorsally exposed portion of the premaxilla, the average for the *A. a. pfizenmayeri* specimens is 19.6 (18.0, 20.4 and 20.4) per cent compared to 38.7 (22.5–49.7) per cent for *A. a. gigas*. The former falls beyond the limits for two standard deviations for the latter ($2S = 38.7 \pm 16.20$). A more detailed study of the relationships of these two races must await the availability of adequate series of specimens. In the meantime, however, it seems reasonable to consider them as distinct races.

Specimens Examined. A total of three as follows:

Russia: Junction of Aldan and Lena Rivers, 1 (U.S.N.M.); Central Siberia near Krasnoyarsk, 1 (A.M.N.H.), and Berosovka R. 200 mi. N. Sredne—Kolymsk, 1 (A.M.N.H.).

ALCES ALCES GIGAS Miller
Alaskan Moose

1899. *Alces gigas* Miller, Proc. Biol. Soc. Wash., vol. 13, p. 57.
1901. *Alces machlis gigas* Lydekker, Great and Small Game of Europe, etc., p. 49.
1902. *Paralces gigas* Allen, Bull. Am. Mus. Nat. Hist., vol. 16, p. 160.
1904. *Alces americanus gigas* Osgood, N. Am. Fauna, no. 24, p. 29.
? 1907. *Alces columbae* Lydekker, Field, vol. 9, p. 182 (thought at first to be from somewhere in British Columbia).
1915. *Alces alces gigas* Lydekker, Cat. Ungulate Mamm., Brit. Mus. (Nat. Hist.), vol. 4, p. 237.
1924. *Alces gigas* Miller, U.S. Natl. Mus., bull. 128, p. 491.
1929. *Alces americana gigas* Anderson, Natl. Mus. Can., bull. 56, p. 105.
1950. *Alces americana gigas* Peterson, Roy. Ont. Mus. Zool., Occ. Pap. no. 9, p. 3.

Type Specimen. U.S. National Museum, no. 86166.

Type Locality. North side of Tustumena Lake, Kenai Peninsula, Alaska.

Geographical Distribution. Forested areas of Alaska, western Yukon and northwestern British Columbia.

Characters. Miller (1899), in his original description, gave the following (pp. 57–58):

A larger, more richly colored animal than the eastern moose. Skull with occipital portion narrower, palate broader, and mandible much heavier than in *Alces americanus*.

Color—General color a grizzle of black and woodbrown darkening along spine and changing abruptly to clear black on chest, buttocks, and lower part of sides. Median line of belly hairbrown. Legs hairbrown or broccoli-brown with darker

shading. Head like back, but more finely grizzled. Ears yellowish white internally, broccoli-brown externally.

Skull and teeth—The skull of *Alces gigas* differs from that of *A. americanus* in its larger size and greater massiveness, as well as in certain details of form. Chief among the latter is the great breadth of the palate, relatively to the length of the toothrow. In three males of *A. gigas* the ratio at least palatal breadth (between anterior premolars) to length of toothrow is respectively 47.1, 47.1, and 44.7. In three males of *A. americanus* it is only 36, 36, and 39. In this respect *Alces gigas* resembles *Alces alces*, though the Alaskan animal shows no approach to the conspicuous deepening of the antorbital portion of the skull, or the peculiar form of the premaxillary characteristic of the European species. The occiput is relatively higher and narrower than in *A. americanus*. In two males of the latter the ratio of depth between inion and lower lip of foramen magnum to greatest width across paroccipital processes is 68.5 and 72.2, while in three of *A. gigas* it is 81.8, 84.8 and 87.5.

Remarks. Although described and accepted by several authors as a distinct species (Miller, 1924 and others) it appears, on the basis of skulls from northwestern British Columbia and southern Yukon examined by the writer, to be only subspecifically different since intergradation seems apparent (Peterson, 1950). Lydekker (1915), Osgood (1904), Anderson (Laing and Anderson, 1929, Anderson, 1947), Hall (1934 and 1936) and others have suggested this possibility. Presumably, Miller (1899) used *A. a. americana* material for comparison with the Alaska race, although his chief character for distinguishing *gigas* (least width of palate between toothrow relative to length of toothrow crowns) still remains valid when comparing other North American races (see fig. 2A and table I). With respect to the shape of the occiput, Miller's character holds good for separating *A. a. gigas* from *A. a. americana*, but not from *A. a. andersoni* and *A. a. shirasi*, if the mastoid width is used, which appears a more precise measurement than the width across the paroccipital processes (see fig. 2B). If the height of the occiput alone is compared, *A. a. gigas* appears distinctly greater. "Nine middle-aged adult bulls of the latter averaged 134.1 ± 1.31 mm., while four cows averaged 127.2 ± 1.51 mm. Corresponding measurements of 22 *A. a. andersoni* bulls were 125.2 ± 0.98 mm., while 14 cows averaged 115.1 ± 1.23 mm." (Peterson 1950, p. 3). Specimens of *A. a. americana* and *A. a. shirasi* averaged slightly less than *andersoni*. For a list of the specimens examined which showed apparent intergradation see "Remarks" under *A. a. andersoni*.

Specimens Examined. A total of 38 as follows:

Alaska: Funny River, Kenai Peninsula, 4 (A.M.N.H.) and 1 (C.N.H.M.); Rainy Pass, Kenai Peninsula, 3 (A.M.N.H.); Tustumena L., Kenai Pen-

insula, 1 (U.K.) and 1 (U.S.N.M.); Kelly River, Kenai Peninsula, 1 (C.N.H.M.); near Kassilof L., (Tustumena L. ?) Kenai Peninsula, 3 (C.N.H.M.); Kenai Peninsula (no definite loc.), 2 (A.M.N.H.), 2 (B.S.C.), 1 (Carn. M.), 1 (C.N.H.M.), 2 (U.K.); 18 mi. s. McCarthy, 1 (B.S.C.); Coleville R., 1 (B.S.C.); Chugachik Bay, 2 (A.M.N.H.); Mt. McKinley, 1 (B.S.C.).

British columbia: Dease R., McDame Post, 1 (B.S.C.); Atlin, 2 (B.C.P.M.).

Yukon: Teslin River district, 2 (N.M.C.); N. Teslin Lake, 1 (N.M.C.); Harris Cr., Headwaters White R., 1 (B.S.C.); Kletson Cr. (Trib. White R. ?), 1 (D.M.N.H.).

ALCES ALCES SHIRASI Nelson
Yellowstone Moose

1914. *Alces americanus shirasi* Nelson, Proc. Biol. Soc. Wash., vol. 27, p. 72.
1924. *Alces americana shirasi* Miller, U.S. Natl. Mus., bull. 128, p. 490.
? 1907. *Alces columbae* Lydekker, Field, vol. 9, p. 182 (British Columbia ?).

Type Specimen. U.S. National Museum, no. 202975.

Type Locality. Snake River, Lincoln County, Wyoming.

Geographical Distribution. Western Wyoming, eastern and northern Idaho, western Montana, northward into southwestern Alberta and southeastern British Columbia. Occasional occurrence in extreme northeastern Utah has been reported by Durrant (1952).

Characters. "Differs strongly in early winter pelage from typical *Alces americanus* from Maine, Nova Scotia, and New Brunswick in having the entire top of the back, including upper side of neck rather pale rusty yellowish-brown, slightly washed on tips of hairs with dusky; ears paler and grayer; hoofs much smaller and shorter" (Nelson, 1914, p. 72). Hall (1934) was not able to substantiate the smallness of feet. In his original description Nelson (1914) was unable to find any appreciable cranial difference between typical *A. a. americana* and *A. a. shirasi*, although when considering measurements shown in fig. 2 there can be little doubt of significant difference between these two. It approaches closer to *A. a. andersoni* but on the basis of specimens examined, including the type of *A. a. shirasi*, it differs in having a greater degree of flare of the nasal aperture. The length of the upper toothrow crowns averaged the shortest of all races (see table I).

Remarks. The colouring of the pelage along the withers and dorsal portion of the back has been pointed out by Nelson as the most distinctive character of this race. Great difficulty is encountered in making critical colour comparisons because of the impracticability of examining sufficient specimens in series.

Although there is much variation in coloration, especially with respect to seasonal changes, this race appears to represent the extreme in light coloration along the back, among North American forms. In addition to being more extensive, this light area lacks the rufus tones usually present in *A. a. andersoni* (based on late fall specimens). The Alaskan race also has a fairly extensive area of paler coloration along the withers and back, but it is much less distinct and usually appears darker with a more brownish or reddish tint than *A. a. shirasi*. This light area is apparently least extensive in *A. a. americana*. For a list of specimens showing apparent intergradation see "Remarks" under *A. a. andersoni*.

Specimens Examined. A total of 34 as follows:

Alberta: Banff, 1 (U.S.N.M.); Waterton, 1 (U.B.C.).

British Columbia: 4 or 5 mi. below Ochre Cr., 1 (U.S.N.M.); Vermilion R., 1 (B.S.C.); Fraser R., 1 (B.S.C.); Golden. 1 (U.B.C.).

Colorado: Grand Co., 1 (D.M.N.H.).

Idaho: Selway area, 2 (U. Mont.).

Montana: Upper Missouri R., 1 (U.S.N.M.); Gallatin Canyon, Yellowstone National Park, 1 (M.S.C.); near Gardiner, Park Co., 1 (U. Mont.); 20 mi. S. Anaconda, Deer Lodge Co., 1 (Carn. M.); 8 mi. S. Wise R., Beaver Head Co., 2 (Carn. M.); 10 mi. N. Polaris, Beaver Head Co., 1 (Carn. M.).

Wyoming: Teton Canyon, 1 (U.S.N.M.); Teton Co., 1 (B.S.C.), 1 (U. Mich.); S. Fort Buffalo Cr., Teton Co., 1 (A.N.S.P.); near Jackson, 1 (U.S.N.M.); Bridge L., S. of Yellowstone Park, 3 (A.M.N.H.); near Hawk's Nest, Upper Yellowstone, 1 (A.M.N.H.); Yellowstone National Park, 4 (Y.N.P.), 1 (R.O.M.Z.P.); S. Ft. Shoshone R., near Cody, 1 (U.S.N.M.); Snake R., Lincoln Co., 3 (B.S.C.).

ALCES ALCES ANDERSONI Peterson
Northwestern Moose

1950. *Alces americana andersoni* Peterson, Roy. Ont. Mus. Zool., Occ. Pap. no. 9, p. 1, May 25.

? 1907. *Alces columbae* Lydekker, Field, vol. 9, p. 18a (British Columbia ?).

? 1907. *Alces columbae* Lydekker, Zool. Rec., vol. 44, Mamm., p. 69 (Ontario ?).

? 1915. *Alces alces columbae* Lydekker, Cat. Ungulate Mamm., Brit. Mus. (Nat. Hist.), vol. 4, p. 236 (Ontario ?).

Type Specimen. Adult male (skin and complete skeleton) no. 20068, Royal Ontario Museum of Zoology and Palaeontology, collected by Mr. F. D. de Delly on December 18, 1949.

Type Locality. Section 27, Township 10, Range 16, Sprucewood Forest Reserve (15 mi. E. Brandon), Manitoba.

Geographical Distribution. Northern Michigan and Minnesota, western Ontario, westward to central British Columbia, north

to eastern Yukon Territory and Mackenzie Delta, Northwest Territories.

Characters. Differs from *A. a. americana* in having a greater width of palate (as measured between the upper toothrows) relative to the length of the upper toothrow crowns. In a series of skulls of 24 middle-aged bulls the least width of palate averaged 38.3 ± 0.46 per cent of the length of the toothrow compared to 35.6 ± 0.56 in 21 similarly aged bulls of *A. a. americana* (see fig. 2A). In similar measurements of cows 16 *A. a. andersoni* specimens averaged 37.7 ± 0.56 compared to 33.7 ± 1.22 for 11 specimens of *A. a. americana.* Also differs from the latter by possessing a relatively higher and narrower occiput (as measured from the inion to the lower lip of the foramen magnum) relative to the mastoid width. A series of 22 middle-aged bulls averaged 76.8 ± 0.77 per cent compared to 73.1 ± 0.63 per cent in 15 males of *A. a. americana.* In 13 cows of the former the average was 81.5 ± 0.71 compared to 76.6 ± 1.02 for 11 of the latter (see fig. 2B). In bulls the nasal aperture of 25 specimens showed a distinct difference from 23 *A. a. americana* by being more widely flaring, although no significant difference between the cows of these two races was found in this case (see fig. 2C). In middle-aged cows, however, a distinct difference in the ratio of the mastoid width relative to the greatest zygomatic breadth was found with 13 specimens averaging 73.0 ± 0.76 per cent compared to 76.2 ± 0.65 in 11 skulls of *A. a. americana.* In this character bulls did not appear significantly different. Similarly the cows also differ by having a relatively shorter and wider rostrum when the greatest antorbital breadth is compared with the median palatal length. The former averaged 44.8 ± 0.56 per cent of the palatal length in 15 cows compared to 42.6 ± 0.39 in 11 *A. a. americana* females. In bulls similar measurements were 45.0 and 43.5 per cent respectively, but a slight overlap of this character was noted.

Differs from *A. a. shirasi* in having a narrower and less flaring nasal aperture. In the latter the difference between the greatest inside width of the nasal aperture and the width at the junction of nasals averaged 29.9 ± 0.64 mm. in 10 middle-aged males and 26.3 ± 1.37 mm. in six females of similar age while the corresponding measurement for *A. a. andersoni* was 24.1 ± 0.84 for 25 males and 20.5 ± 1.02 for 16 females. When these measurements are compared to the length of the nasal aperture, a significant difference is found between these two races (fig. 2C).

In bulls *A. a. andersoni* differs from *A. a. shirasi* in having a relatively longer toothrow, averaging 149.8 ± 0.73 in 24 middle-aged specimens of the former and 142.9 ± 1.83 in 11 of the latter. Further difference is found in bulls in the least width of the palate between the toothrow relative to the length of upper toothrow crowns (fig. 2A) although in both tooth characters, overlapping was found in the smaller number of cows examined.

A. a. andersoni differs from *A. a. gigas* in having a much narrower least width of palate between toothrows relative to the length of the upper toothrow crowns (fig. 2A) and in having a lower occiput as measured from the inion to the lower lip of the foramen magnum. Nine middle-aged adult bulls of the latter averaged 134.1 ± 1.31 mm. while four cows averaged 127.2 ± 1.51 mm. Corresponding measurements of 22 *A. a. andersoni* bulls were 125.2 ± 0.98 while 14 cows averaged 115.1 ± 1.23 mm.

In colour, *A. a. andersoni* appears intermediate between *A. a. americana* and *A. a. shirasi* with usually more light rufus tones appearing on the head and back region in fall specimens, although much variation is found with the seasons; light area of shoulder hump region usually more extensive than the former and less extensive than the latter. Hall (1936) came to similar conclusions regarding a specimen from Bowron Lake, British Columbia. Observations in the field give the impression that *A. a. americana* has a heavier and shorter neck. A check on the cervical vertebrae of one specimen from eastern Ontario and two from western Ontario (all with comparably sized skulls) indicated no significant difference in the length of the centra although each vertebra of the eastern form was consistently the heavier and wider. A further correlation of this condition is suggested in the relatively wider occiput (fig. 2B) of *A. a. americana*.

Remarks. Hall (1934) found that in moose from Bowron Lake, British Columbia, the least width of the palate amounted to 40 (39–42) per cent of the crown length of the upper toothrows in bulls and 36 (32–37) per cent in cows, while in two specimens from Minnesota the bull was 37 per cent and the cow 34 per cent. These measurements fall within the limits for *A. a. andersoni* and thus seem referable to that race. Specimens showing varying degrees of apparent intergradation with other races were examined as follows:

With *A. a. gigas:*

British Columbia: Cassiar Mts., 1 (Carn. M.); Telegraph Creek, 3 (B.C.P.M.) and 1 (D.M.N.H.).

Yukon: MacMillan R., 2 (B.S.C.); Sheep Mt., E. of Atlin L., 1 (C.N.H.M.); N. of Leslin L., 3 (N.M.C.); Teslin R., 3 (N.M.C.).

With *A. a. shirasi:*

Alberta: Saskatchewan R., mi. 109, 1 (U.B.C.); Southesk L., Jasper Park, 1 (U.B.C.).

British Columbia: Field, 1 (U.B.C.); Golden, 1 (U.B.C.).

With *A. a. americana:*

Ontario: Although no mature specimens are presently available from the centre of the zone of overlap of these two races, there seems little doubt that intergradation is taking place along a belt from the north shore of Lake Superior, northward. One yearling male from Flint Lake, 35 mi. E. Longlac exhibits a mixture of characters between *A. a. americana* and *A. a. andersoni*.

Specimens Examined. A total of 132 as follows:

Alberta: Entrance, 1 (A.M.N.H.); Little Smoky R., N. of Jasper Park, 2 (A.M.N.H.); Thoral Cr., 1 (A.M.N.H.); Hay R. Flats, 1 (U. Mich.); Eagle Nest Pass, 1 (Carn. M.); Brazeau R., 175 mi. N.W. Calgary, 1 (Carn. M.); Elk Island Park, 1 (N.M.C.).

British Columbia: Jarvis Pass, 1 (U.S.N.M.); McDame Post, Dease R., 1 (B.S.C.); Takla Landing, 2 (B.C.P.M.); Atlin, 1 (B.C.P.M.); Tupper Cr., 2 (B.C.P.M.); Chezacut, 1 (B.C.P.M.); Ootsa L., 2 (U.B.C.); Caribou Dist., 1 (U.B.C.); Quick, 6 (U.B.C.); Quesnel, 1 (U.B.C.); Telkwa, 1 (U.B.C.); Shesley Mts., 2 (A.M.N.H.); Level Mt., 1 (A.M.N.H.); no definite locality, 5 (U. Kan.) and 1 (A.M.N.H.).

Manitoba: Portage la Prairie, 4 (U.S.N.M.); Hudson Bay R.R. (no definite locality), 1 (U.S.N.M.); Overflowing R., N. of Lat. 53, S. of the Pas, 1 (R.O.M.Z.P.); Sprucewood Forest Reserve, 15 mi. E. of Brandon (type specimen), 1 (R.O.M.Z.P.).

Michigan: Chippewa Harbor, Isle Royale, 3 (U. Mich.); Lake Eva, Isle Royale, 1 (U. Mich.); Houghton Cove, Isle Royale, 5 (U. Mich.); McCargoe Cove, Isle Royale, 3 (U. Mich.) and 2 (A.M.N.H.); no definite locality, Isle Royale, 8 (U. Mich.).

Minnesota: Temperance R., Cook Co., 1 (B.S.C.); Moose R. (?), 2 (U. Kan.); Thief L., Marshal Co., 1 (U. Kan.); Lake of the Woods, 19 (U. Kan.); no definite locality, Northern Minn., 1 (U.S.N.M.) and 1 (M.C.Z.).

Ontario: (Unless otherwise designated specimens are in the Royal Ontario Museum of Zoology and Palaeontology). Whitefish L., Thunder Bay Dist., 1 (A.M.N.H.); St. Ignace Is., L. Superior, 18; Simpson Is., L. Superior, 2; Bead Is., L. Superior, 1; 40 mi. N.W. Port Arthur, 1; Long Bay, Lake of the Woods, 1; Ear Falls, Kenora Dist., 1; Gull Rock L., Kenora Dist., 1; Wabaskank L., Kenora Dist., 1; Nungessor L., Kenora Dist., 1; Narrow L., 20 mi. E. Kenora, Kenora Dist., 1; Sioux Narrows, Kenora Dist., 1; no definite locality, Kenora Dist., 1.

Saskatchewan: Birch L., 1 (N.M.C.); Harper L., 1 (N.M.C.).

Yukon Territory: Ross R., Canol Rd., mi. 95, 1 (N.M.C.); Lapie R. (Canol Rd.?) mi. 120, 1 (N.M.C.); Teslin Dist., 3 (N.M.C.).

ALCES ALCES AMERICANA (Clinton)
Eastern Moose

1822. *Cervus americanus* (Clinton), Letters on Nat. Hist. and Int. Resources of New York, p. 193.
1835. *Alces americanus* Jardine, Nat. Library, vol. 21 (Mammalia; deer, antelope, camels, etc.), p. 125.
1846. *Cervus lobatus* Agassiz, Proc. Boston Soc., vol. 2, p. 188.
1852. *Alces muswa* Richardson, Zool. Herald, Mamm., p. 66.
1873. *Alces lobata* Fitzinger, Sitzber. K. Ak. Wiss. Wien, vol. 68, pt. 1, p. 348.
1884. *Alce americanus* Merriam, Mammals of Adirondacks, p. 138.
1885. *Alces machlis* True, U.S. Natl. Mus., vol. 7, p. 592.
1901. *Alces machlis americanus* Lydekker, Great and Small Game of Europe, etc., p. 46.
1902. *Paralces americanus* Allen, Bull. Am. Mus. Nat. Hist., vol. 16, p. 160.
? 1907. *Alces columbae* Lydekker, Zool. Rec., Vol. 44, Mamm., p. 69 (Ontario ?).
? 1915. *Alces alces columbae* Lydekker, Cat. Ungulate Mamm., Brit. Mus. (Nat. Hist.), vol. 4, p. 236 (Ontario ?).
1915. *Alces alces americanus* Lydekker; *op. cit.*, p. 234.
1924. *Alces americana americana* Miller, U.S. Natl. Mus., bull. 128, p. 490.

Type Specimen. Unknown.

Type Locality. "Country north of Whitestown" (probably in the western Adirondack region), New York.

Geographical Distribution. From Maine and Nova Scotia westward through Quebec to central northern Ontario where it apparently intergrades with *A. a. andersoni.*

Characters. Differs from other moose in having a narrower palate relative to length of toothrow. Differs from *A. a. andersoni* by possessing a relatively lower and wider occiput (as measured from the inion to the lower lip of the foramen magnum, relative to the mastoid width). In colour it usually appears darker than the latter in late fall coat with deeper brown tones instead of the lighter rufus of *A. a. andersoni.* The extent of light coloration on the withers apparently averages the least of all North American races.

Specimens Examined. A total of 64 as follows:

Maine: Eustis, 1 (U.S.N.M.); Umbagog L., 1 (M.C.Z.); Megantic, 1 (M.C.Z.); no definite locality, 4 (M.C.Z.) and 1 (D.M.N.H.).

New Brunswick: Fredericton, 1 (U.S.N.M.); Nepisiquit, 1 (U.S.N.M.); Chipman, 1 (U.S.N.M.); Bolt Mt. near Newcastle, 1 (U.S.N.M.); Gloucester Co., 1 (N.M.C.); Bald Mt., 1 (B.S.C.); Trousiers L., 1 (A.M.N.H.); no definite locality, 2 (B.S.C.); 1 (A.M.N.H.) and 1 (Carn. M.).

New York: Adirondacks, 1 (U.S.N.M.).

Nova Scotia: Bear R., 1 (B.S.C.) and 1 (M.C.Z.); Guysboro Co., 4 (B.S.C.); Head of Roseway R., 1 (B.S.C.); Kedgemakwoge L., 3 (B.S.C.); no definite locality, 1 (M.C.Z.).

Ontario: (Unless designated otherwise, specimens are in the Royal Ontario Museum of Zoology and Palaeontology). Mackay, Renfrew Co., 1 (U.S.N.M.); Stonecliff, Renfrew Co., 1 (U.S.N.M.); Mattawa, Nipissing Dist., 1 (M.C.Z.); 250 mi. N.W. Sault Ste Marie, 1 (Carn. M.); S.W. boundary Algonquin Park, 1; S.W. sect. of Algonquin Park, 1; Long L., Algonquin Park, 1; Upper Ottawa R., 1; Cavendish Twp., Peterborough Co., 1; Twp. 11B, Sudbury Dist., 1; Nemagos, Halsey Twp., Sudbury Dist., 1; Twp. 13H, Sudbury Dist., 1; Sadler Twp., Sudbury Dist., 1; Twp. 11G, Sudbury Dist., 1; Raney Twp., Sudbury Dist., 1; Twp. 12G, Sudbury Dist., 1; 15 mi. S. Kapuskasing, Cochrane Dist., 1; Kapuskasing Twp., Cochrane Dist., 1; Mowbray Twp., Cochrane Dist., 1; Twp. 46, Algoma Dist., 1; Hayward Twp., Algoma Dist., 1; Walls Twp., Algoma Dist., 1, and Cobden Twp., Algoma Dist., 1.

Quebec: Teiton Clut (?), 1 (U.S.N.M.); Two Rivers (?), 1 (U.S.N.M.); Sandy Creek, 4 (N.M.C.); Spruce Grove, Pontiac Co., 2 (N.M.C.); Temiskasing L., 1 (R.O.M.Z.P.); Fumerton L., 50 mi. N.W. Amos, 1 (R.O.M.Z.P.).

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